

Antler casting in relation to parturition in semi-domesticated female reindeer

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Abstract: We investigated the timing of the right and left antler casting in semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) in relation to parturition using 139 antlered adult individually marked females in 2008–09 between May 5 and June 2; a period when all calves were born and all females cast their antlers. We analysed time of casting of right and left antler in relation to pregnancy, female age and body weight, weight and sex of the calf, and birth date. Seven of the females were non-pregnant (barren) and cast their antlers during the second week of May and at the same time as some of the females that gave birth initiated antler casting. Postpartum retention of antlers varied from 0 to 15 days. We found no difference between left and right antler casting schedule and within two days apart, 91% of the females had cast both antlers. The maximum number of antler castings per day occurred on the seventh day after parturition. Of the 132 females that gave birth, 7 females (5.3%) cast both antlers 5–23 days before calving, three females cast right antler 6–10 days before and the left antler 2–5 days after calving and one female that bore only a left antler casted a day before calving. Antler casting among lactating females was related only to female age, indicating that older females cast antlers earlier than younger females (i.e. 3 days earlier than the pooled mean of 7.6 days). Apart from calving date being two days later among the 7 females that alternated their casting schedule, female body weights, calf sex and calf birth weight among them did not differ between the two years. We conclude that it is a small but consistent antler casting overlap between barren and pregnant/lactating females, indicating that the control mechanism for casting of antlers is not “fool proof” and that antler status prior to parturition does not accurately predict pregnancy status in this domestic reindeer group.

Key words: antler casting; parturition; pregnant females; barren females; semi-domesticated reindeer; *Rangifer t. tarandus*.

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Introduction

In most deer species (Cervidae), growth of antlers is a male secondary sexual characteristic. The single exception is reindeer and caribou (*Rangifer tarandus*) in which both sexes produce antlers and therefore provide a particularly in-

teresting case when studying dominance relationships. However, relative antler size serves as a secondary sexual characteristic in this species because female antlers are relatively smaller than those of males.

The annual energetic and nutritional toll of

antler renewal (Goss, 1983) suggests that selection would have suppressed this trait if it were not advantageous for the individuals. The antlers of female reindeer have probably been both evolved and retained because of their gregarious behavior and the stressful conditions in winter compared to other cervids (Henshaw, 1968; Espmark, 1971; Roberts, 1996; Geist, 1999). Carrying their antlers all winter seems to give females a clear advantage in competition for food in that critical season (Barrette & Vandal, 1986). Dominance relationships in female groups of semi-domesticated reindeer relate to age, antler size and body size (Kumpula *et al.*, 1990). In a follow up study Kumpula *et al.* (1992) found the dominance relationships in female reindeer groups changed after antler removal and suggested that intra-herd competition in winter may have favored antler development in female reindeer. Later, Holand *et al.* (2004) investigated the influence of body mass, antler size and age on social rank and concluded that both body mass and age are good predictors of social rank in female reindeer, whereas antler size in comparison plays a less important role in herds with a “normal” female age structure. This suggested that female antlers may have evolved in inter-sexual rather than intra-sexual competition. However, phenotypes without antlers occur regularly in all populations, although their frequency varies greatly (Reimers, 1993; Schaefer & Mahoney, 2001) thus indicating a less clear cut relationship between antlers and dominance.

The phenology of antler casting in female reindeer and caribou is not simple and seems to be related to parturition (Espmark, 1971). The timing of the right and left antler casting and the overall strong relationship of antler casting to parturition indicating an endocrine control, possibly steroid levels as recorded among reindeer calves (Blake *et al.*, 1998). Non-pregnant females usually cast antlers a few weeks before the calving season, whereas pregnant females

cast a few days after giving birth (Lent, 1965; Espmark, 1971; Bergerud, 1976). As most adult males are absent from the calving groups at this time (Thomson, 1977) this intra-sex difference in antler casting is intriguing.

This study is a follow up of Espmark (1971) to further investigate female reindeer antler casting schedule in relation to parturition as previous findings are either conflicting or inconclusive.

Methods

In conjunction with a population genetic study in an experimental reindeer herd in Kaamanen in northern Finland (69°10'N) during the calving seasons in 2008 and 2009, a total of 139 antlered adult individually marked females, of which 7 were non pregnant (barren), were observed between May 5 and June 2. During this period all calves were born and all females cast their antlers. The age of the females was between 2 and 14 years. During the winter months reindeer were in supplementary feeding (silage and concentrates, Poronherkku, Raisio) both years in the forest area. The female age and body weight, birth date, weight and sex of the calf, antler status and time of casting of right and left antler were recorded. Prior to model testing we ran t-tests to resolve the question of possible differences in antler casting schedule between left and right antler. We found no difference and decided to run linear mixed-effects models (LMM) of antler casting after birth (left and right combined) fitted with individual and year as random effects to control for repeated measures. Antler casting may vary with female age at parturition, weight before calving, and offspring sex and weight. To control for these variations we fitted these as fixed-effect factors in the models.

We also produced the probability plots for calving dates and antler casting schedule (casting vs. no casting) in relation to dates (*i.e.* as predictor variable) from May 1 to June 2 using

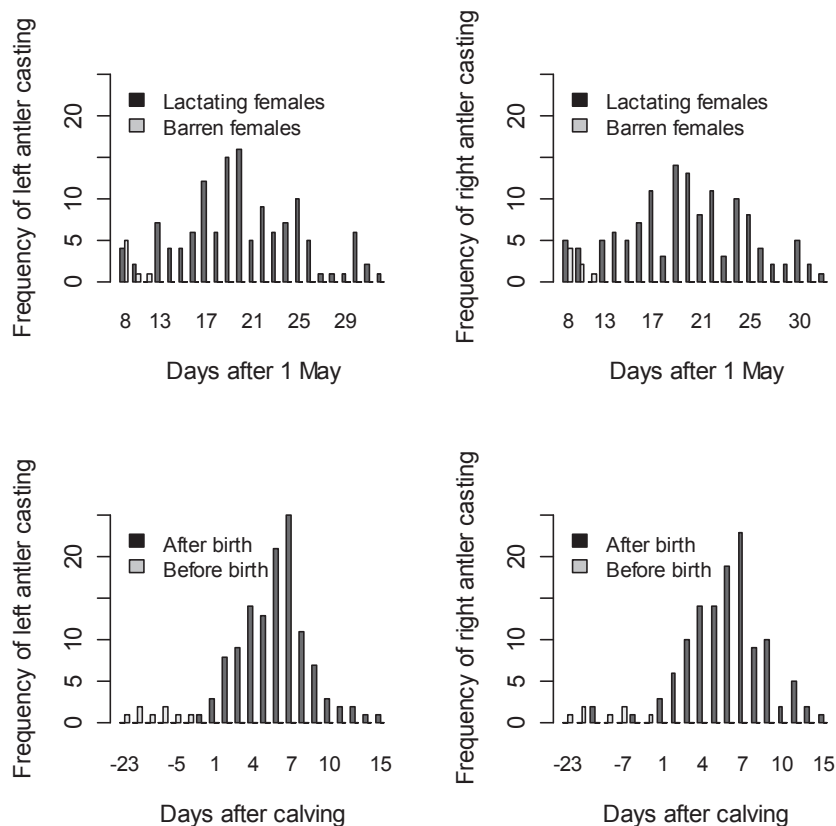


Fig. 1. Antler casting schedule among adult 2+ year old domestic reindeer females in Kaamanen, Finland in 2008 and 2009.

logistic regression. All analyses were done in R version 2.15.1 (R Development Core Team, 2012).

Results

Among the 139 antlered females, two of which were antlerless on one side and seven of the two-antlered were barren and cast their antlers during the second week of May (Fig 1.).

Of the 132 females that gave birth, 7 females (5.3%) cast both antlers 5 – 23 days before calving, three females cast right antler 6 – 10 days before and the left antler 2 – 5 days after calving and one female bore only a left antler that were cast one day before calving (Fig. 1).

We found no significant difference between

left and right antler casting schedule ($t = 0.28$, $P = 0.78$) among females that gave birth. Sixty percent of the females that gave birth and that carried two antlers cast both antlers on the same day, 21% one day apart, 10% two days apart and the remaining 8% between three and 11 days apart (Fig. 2).

Antler casting among lactating females was related only to female age, indicating that older females cast antlers earlier than younger females (*i.e.* 3 days earlier than the pooled mean of 7.6 days; $t = -2.84$, $P = 0.01$). Other possible influential factors like female body weight in April, calf body weight or sex did not influence antler casting and were removed from the final model ($P > 0.05$). Logistic regression plots (Fig 3A, B)

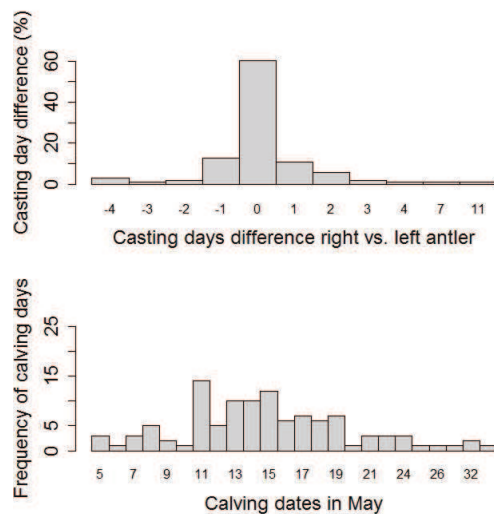


Fig. 2. Number of days difference between antler casting of right vs. left antler and calving dates in May among adult 2+ year old domestic reindeer females in Kaamanen, Finland in 2008 and 2009.

depicts that both calving day and antler casting schedule show similar trend with increasing days from May 1 to June 2. However, antler casting schedule reached maximum threshold few days earlier than the average calving date indicating that some of the female reindeer cast their antler before calving.

Calving occurred earlier in 2009 than in 2008 (Fig. 2); median date 13th of May vs. 16th of May. Median calving date in a pooled sample from both years was 14th of May. Females that gave birth in 2008 cast their left and right antler 7 days postpartum vs. 5 days postpartum in 2009.

Among the 139 antlered females, 54 individual females were sampled in 2008 and again in 2009 and made possible an evaluation of individual antler casting schedule in two consecutive years. All of them gave birth but antler casting schedule was different. Only one female cast both antlers before calving (13 days) in 2008 while the remaining 53 cast their antlers after calving. In 2009 the one female that cast 13 days before calving cast antlers two days af

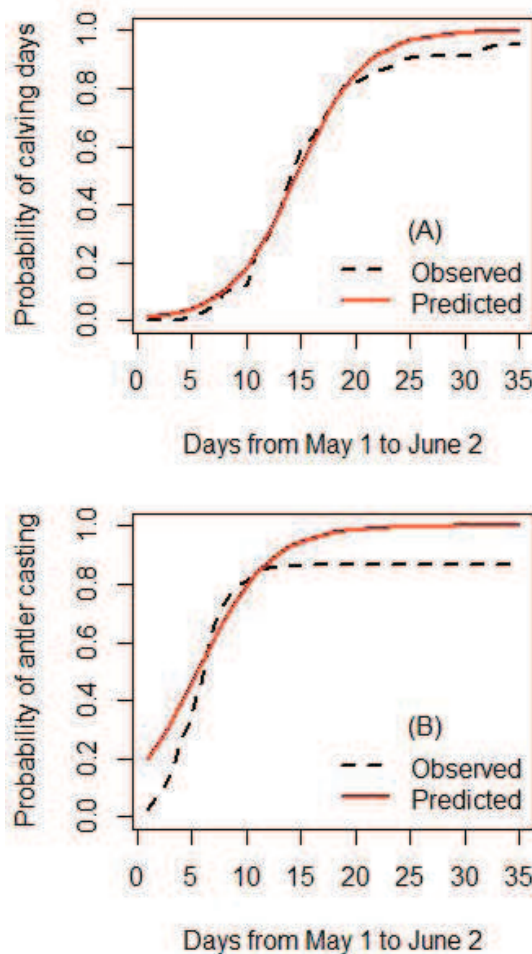


Fig. 3. Probability of calving days and antler casting schedule among adult 2+ year old domestic reindeer females in relation to days from May 1 to June 2 fitted with logistic regression.

ter calving but 6 females that cast antlers after calving in 2008 cast their antlers before calving.

Discussion

There was an overlap in antler casting between the antlered barren and pregnant females and some pregnant females also cast their antlers before giving birth. In a study of individually marked females, Espmark (1971) recorded the exact casting schedule of 45 antlered pregnant females and found that casting took place 1-11 days and a mean at 5-6 days post parturition.

While none of the pregnant females in the Espmark (1971) study cast antlers before calving, one out of 54 in 2008 and 6 out of 54 in 2009 in our study cast their antlers before calving. The recorded overlap in antler casting pattern support earlier findings both among reindeer (Sokolov, 1959; Wika, 1980; Leader-Williams, 1988) and caribou (Lent, 1965; Kelsall, 1968; Skoog, 1968; Bergerud, 1976; Thing *et al.*, 1986). Such deviations in dates of antler casting may be more common than previously acknowledged. In a large herd of caribou studied during the 1986 calving season in Quebec-Labrador, Canada, Gagnum & Barrette (1992) found that, contrary to expectations, a high proportion of females (13.5%) cast their antlers ≥ 2 weeks before giving birth.

Antler casting schedule among lactating females was related to female age indicating that older females cast antlers earlier (3 days) than the pooled mean of 7.6 days. Murie (1935) and Banfield (1954) report corresponding tendency while Espmark (1971) found no significant difference. The majority of lactating female cast antlers postpartum on day 7 in our study and 1 day earlier in Espmark (1971). Inspecting barren ground caribou in Northwest Alaska, Lent (1965) reported that none among 1600 females retained antlers for more than a week postpartum.

We found that 91% of the females had cast both antlers within two days apart, and this schedule corresponds to Espmark (1971) who report that usually both antlers were cast on the same day. Apparently, the overlap of antler casting schedule among lactating and barren reindeer females in spring indicates that the control mechanism for casting of antlers is not “fool proof” and that some environmental factors may interact. Our knowledge of the underlying development and endocrine mechanisms in reindeer is limited. Annual endocrine profiles in adults (Bubenik *et al.*, 1997; Borisenkov, 2001) and studies on the effects of gonadec-

tomy in both adults (Lincoln & Tyler, 1994) and calves (Lincoln & Tyler, 1999) collectively indicate that steroid hormones, testosterone in males and estradiol in females, are important regulators of the reindeer antler cycle (Blake *et al.*, 1998). The ability of testosterone and estradiol to prevent the old antlers from being cast, to inhibit new ones from regenerating, and to cause the velvet to cast prematurely from growing antlers may be taken to indicate a general tendency of either sex hormone to bring about or to preserve the mature condition of antlers (Goss, 1968) supporting a hypothesis put forward by Wislocki *et al.* (1947). Estradiol stimulates the growth and mineralization of the antler bone and the cleaning of the velvet (Lincoln & Tyler, 1999). Whether estradiol also suppresses the casting of the hard antlers as suggested by Lincoln & Tyler (1999) is uncertain as Shipka *et al.* (2007) report estradiol at baseline concentrations until approximately 24 week of gestation and rising coincidentally as progesterone declined just before parturition. Although uncertainty as to the detailed control mechanism the steroids apparently act to synchronize the antler cycle to the seasonal reproductive cycle with the hard antlers functioning as weapons and social signal both in intra-sexual and inter-sexual competition in winter and in spring (Lincoln & Tyler, 1994).

The endocrine control ensures that the hard antlers are retained throughout the autumn and winter when the females are normally pregnant and when competition over food and food craters in the snow is most intense. Casting antlers on the calving ground also provides females with a supply of minerals at a time of likely mineral deficiency after parturition and a long winter of feeding on mineral-poor lichens, and great mineral need at the beginning of lactation (Wika, 1982; Barrette, 1985) and during antler growth (Baksi & Newbrey, 1989).

We conclude that it is a small but consistent antler casting overlap between barren and preg-

nant/lactating females in this domestic reindeer group and that antler casting within same female group may vary between years. Although we have no individual control of antler casting schedule in wild reindeer females, antler size data from four wild reindeer areas in southern Norway over the past 22 years indicate that barren females cast their antlers before the calving season (based on the size of their new antlers and no calf at foot) (Reimers, 2006) and E. Reimers (unpublished data).

One substantially important question remains: despite the systemic endocrine control of the antler cycle, what local factors may interact with antler casting pattern in barren and pregnant/lactating female *Rangifer*? Explanatory candidates include ecotypes (e.g. semi-domestic or wild *Rangifer*), nutrition, and availability of minerals. Individually recorded antler casting is all with semi-domestic reindeer on supplementary feeding in winter (our study) and in fenced in areas which may impact natural behavior, physiology and antler casting schedule during the calving season. Presence or absence of male reindeer in the enclosures may also be an interacting factor.

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References

- Baksi, S. N. & Newbrey, J. W. 1989.** Bone metabolism during antler growth in female caribou. — *Calcif Tissue Int* 45: 314-317.
- Banfield, A. W. F. 1954.** Preliminary investigation of the barren ground caribou. Part II. Life history, ecology, and utilization. *Wildlife Management Bulletin Serie 1*, 10B. 112 pp.
- Barrette, C. 1985.** Antler eating and antler growth in wild Axis deer. — *Mammalia* 49: 491-499.
- Barrette, C. & Vandal, D. 1986.** Social Rank, Dominance, Antler Size, and Access to Food in Snow-Bound Wild Woodland Caribou. — *Behaviour* 97: 118-146.
- Bergerud, A. T. 1976.** Annual Antler Cycle in Newfoundland Caribou. — *Can Field-Nat* 90: 449-463.
- Blake, J. E., Rowell, J. E. & Suttie, J. M. 1998.** Characteristics of first-antler growth in reindeer and their association with seasonal fluctuations in steroid and insulin-like growth factor 1 levels. — *Can J Zool* 76: 2096-2102.
- Borisenkov, M. F. 2001.** Hormonal regulation of antler growth in reindeer, *Rangifer tarandus*. — *Zool Zh* 80: 1139-1143.
- Bubenik, G. A., Schams, D., White, R. J., Rowell, J., Blake, J. & Bartos, L. 1997.** Seasonal levels of reproductive hormones and their relationship to the antler cycle of male and female reindeer (*Rangifer tarandus*). — *Comp Biochem Physiol B Biochem Mol Biol* 116: 269-277.
- Espmark, Y. 1971.** Antler shedding in relation to parturition in female reindeer. — *J Wildl Manage* 59: 584-594.
- Gagnon, L. & Barrette, C. 1992.** Antler casting and parturition in wild female caribou. — *J Mammal* 73: 440-442.
- Geist, V. 1999.** Deer of the world. Their evolution, behaviour and ecology. *San-Hill Press, London*.
- Goss, R. J. 1968.** Inhibition of growth and shedding of antlers by sex hormones. — *Nature* 220: 83-85.
- Goss, R. J. 1983.** Deer antlers. Regeneration, function and evolution. *Academic Press, New York*.
- Henshaw, J. 1968.** A theory for the occurrence of antlers in females of the genus *Rangifer*. — *Deer* 1: 222-226.
- Holand, O., Gjostein, H., Losvar, A., Kum-**

- pula, J., Smith, M. E., Roed, K. H., Nieminen, M. & Weladji, R. B. 2004. Social rank in female reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. — *J Zool (Lond)* 263: 365-372.
- Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. *Canadian Wildlife Service, Ottawa, Canada*.
- Kumpula, J., Kumpula, K. & Nieminen, M. 1990. Dominance relationships in female reindeer groups of semi-domesticated reindeer changes after antler removal. — *Rangifer*, 10, special Issue No. 5: 18.
- Kumpula, J., Kumpula, K. & Nieminen, M. 1992. Dominance relationships among female semi-domesticated reindeer: The function of antlers. — *Rangifer* 12: 173-174.
- Leader-Williams, N. 1988. Reindeer on South Georgia. The ecology of an introduced population. *Cambridge University Press, Cambridge*.
- Lent, P. C. 1965. Observations on Antler Shedding by Female Barren-Ground Caribou. — *Can J Zool* 43: 553-558.
- Lincoln, G. A. & Tyler, N. J. C. 1994. Role of Gonadal-Hormones in the Regulation of the Seasonal Antler Cycle in Female Reindeer, *Rangifer Tarandus*. — *J Reprod Fertil* 101: 129-138.
- Lincoln, G. A. & Tyler, N. J. C. 1999. Role of oestradiol in the regulation of the seasonal antler cycle in female reindeer, *Rangifer tarandus*. — *J Reprod Fertil* 115: 167-174.
- Murie, O. J. 1935. Alaska-Yukon Caribou. — *N Am Fauna* 54: 1-93.
- R Development Core Team 2012. A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing Vienna, Austria*.
- Reimers, E. 1993. Antlerless Females among Reindeer and Caribou. — *Can J Zool* 71: 1319-1325.
- Reimers, E. 2006. Wild reindeer calf recruitment variations; biology or methodology. — *Rangifer* 26: 7-14.
- Roberts, S. C. 1996. The evolution of hornedness in female ruminants. — *Behaviour* 133: 399-442.
- Schaefer, J. A. & Mahoney, S. P. 2001. Antlers on female caribou: Biogeography of the bones of contention. — *Ecology* 82: 3556-3560.
- Shipka, M. P., Rowell, J. E. & Sousa, M. C. 2007. Steroid hormone secretion during the ovulatory cycle and pregnancy in farmed Alaskan reindeer. — *J Anim Sci* 85: 944-951.
- Skoog, R. O. 1968. Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska. — *Ph.D., University of California*.
- Sokolov, I. I. 1959. Fauna of the U.S.S.R. 1, Mammals. Chapter 3., Ungulates. *Academy of Sciences U.S.S.R., Moscow, Leningrad*.
- Thing, H., Olesen, C. R. & Aastrup, P. 1986. Antler possession by west Greenland female caribou in relation to population characteristics. — *Rangifer* 1: 297-304.
- Thomson, B. R. 1977. The behaviour of wild reindeer in Norway. — *Ph.D., University of Edinburgh*.
- Wika, M. 1980. On growth of reindeer antlers. — In: E. Reimers, E. Gaare & S. Skjennberg (eds.). Proceedings of the Second International Reindeer/Caribou Symposium. Direktoratet for vilt og ferskvannsfisk, *Trondheim, Norway, Roros*. pp. 416-421.
- Wika, M. 1982. Antlers - a mineral source in *Rangifer*. — *Acta Zoologica* 63: 7-10.
- Wislocki, G. B., Aub, J. C. & Waldo, C. M. 1947. The effects of gonadectomy and administration of testosterone propionate on the growth of antlers in male and female deer. — *Endocrinology* 40: 201-224.

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Gevirfelling hos reinsimler i relasjon til kalving

Abstract in Norwegian/Sammendrag: Vi undersøkte tidspunktet for felling av gevirene hos 139 individuelt merkede tamrein (*Rangifer tarandus tarandus* L.) i forhold til kalvingstidspunktet i 2008-09 mellom 5. mai og 2. juni, en periode da alle kalvene ble født og alle simler kastet sine gevir. Vi registrerte tidspunktet for felling av høyre og venstre gevir i forhold til drektighet, simlas alder og kroppsvekt, kalvens fødselsvekt og kjønn og fødselsdato. Syv av simlene var gjeldsimler (ikke drektige) og kastet sine gevir i løpet av andre uken i mai og på samme tid som seks av simlene som fødte kalv kastet venstre gevir og ni av dem kastet høyre gevir. Felling av gevirene etter fødsel varierte fra 0 til 15 dager. Vi fant ingen forskjell i fellingstidspunkt av venstre og høyre gevir og innen to dager hadde 91% av simlene kastet begge gevir. Maksimalt antall gevirfellingene skjedde syvende dag etter fødsel. Av de 132 simlene som fødte kalv, kastet 7 (5,3%) begge gevir 5-23 dager før kalving, tre simler felte høyre gevir 6-10 dager før og venstre gevir 2-5 dager etter fødsel. En simle hadde bare venstre gevir som ble felt en dag før kalving. Gevirfelling blant simler med kalv var kun knyttet til simlenes alder. Eldre simler felte geviret 3 dager tidligere enn samlet gjennomsnitt på 7.6 dager. Vi registrerte gevirfellingsmønsteret hos 54 simler i 2008 og igjen i 2009. Alle fødte kalv de respektive årene, men fellingsmønsteret var forskjellig. I 2008 kastet bare én simle begge gevir før kalving (13 dager), mens de resterende 53 kastet sine gevir etter kalving. I 2009 kastet den simla som kastet 13 dager før kalving sitt gevir to dager etter kalving, men nå kastet seks simler som kastet gevir etter kalving i 2008 sine gevir før kalving. Bortsett fra at kalvingsdatoen var to dager senere blant de syv simler som endret fellingsskjema i forhold til kalvingstidspunkt, var det ingen sammenheng til simlenes alder eller kroppsvekt eller til kalvens kjønn og fødselsvekt. Vi konkluderer med at det er en liten, men gjennomgående overlappende gevirfelling mellom gjeldsimler og drektige/ammende simler, noe som viser at kontrollmekanismen for gevirfelling ikke er "feilfri", og at gevirstatus før fødsel ikke nøyaktig forutsier drektighetsstatus i denne tamreinflukken.